

THE EVOLUTION OF THE ABDOMINAL PATTERN IN TABANIDAE (DIPTERA)¹

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There are certain acknowledged and well-known principles by means of which it can be ascertained whether a given type of pattern is primitive or derived, and by which, among a number of given patterns, the most primitive of them may be determined. A form in which the same elements of pattern are repeated on all segments of the abdomen, and in the same relative position on each of them, will be considered more primitive than a form where this same pattern is found only on one or a few of the segments while the others are of uniform color, or show a different pattern. In the internal as well as in the external anatomy of the segments we possess numerous instances of a specialized development of single segments, a character which is always considered as derived or secondary. In general, though not in all cases, we will then have to assume that characters which potentially existed in all segments, have been preserved and further specialized only in certain of them, while in the others every trace of them has disappeared. Or it may be that the specialization of originally equal elements took place in divergent directions. In the case of abdominal patterns, fusion of spots may take place in one segment, suppression of spots in others, etc. The second characteristic of primitiveness is, consequently, the homeotropic isotropism of pattern, as we may call it: the even distribution of the elements of pattern in the segment and on the whole abdomen, relatively to size, degree of pigmentation, condition, etc., of these elements. If the elements of pattern are evenly distributed over the segment, or its dorsal and ventral surface, we are confronted with a more primitive condition than in the case of an uneven pattern. A pattern consisting of a definite number of spots of the same size and in equal distance from one another, is more primitive than a pattern consisting of large spots on the median line and small or no spots on the sides. The absence of any definite pattern, then, will always have to be considered

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as a derived condition, if it can be shown that existing traces or rudiments of pattern are themselves the remainders of a derived type, so that the possibility is excluded that they might be a sort of pattern *in statu nascendi*. If patterns appear *de novo*, it should be assumed that they will appear in places where the physiological conditions for their appearance are in evidence; it would be astonishing if a pattern would appear as the result of a number of simultaneous but otherwise entirely unrelated changes, while by a single change in the germ plasma either a homogenous coloration, or, if any pattern, a more or less isotropic pattern will be developed, showing at most a relationship to the borders of the segments or other preferential localizations.

These principles are sufficient to classify the abdominal patterns of Tabanidae as to their phylogenetic value or relative degree of evolutionary specialization. It should be kept in mind, however, that here no classification of species is intended; this would be entirely impossible on such basis, as often male and female of the same species represent divergent types of pattern of very different degree of specialization. For the larger groups, subgenera, etc., often a certain degree of specialization is characteristic, but not unfrequently one or two species, or one sex of a species, will show a pattern which is more frequently encountered in another systematic category, lower or higher in the system, as the case may be.

The most primitive type of abdominal pattern which I was able to find in Tabanidae, is found in the genus *Haematopota* and in a number of species of *Tabanus* which are evidently related to *Haematopota*. This pattern consists of alternating dark and light elements of medium size, usually five light spots separated by dark on each segment, so that a light spot occupies the middle of the dorsal side of each segment, while two others, which we may call the sub-dorsal and lateral spots, occupy the sides. One will not expect to find everything perfect and to one's wishes in nature; in fact, even in the most generalized forms of which I found illustrations, this ideal pattern is shown slightly modified, and so, especially on the first and again on the last segments of the abdomen in the example of *Haematopota brunneescens* (fig. 1), an African species, show that the lateral spots are preserved only on

segments one to four, while on segments five to eight they have been swallowed by the dark background. Phenomena of this kind are so frequently observed that they do not detract anything from the soundness of the assumption that the five-spotted segment represents the primitive condition. It seems that processes of reduction of pattern always begin at both ends of the abdomen, but progress more rapidly from the posterior end while the middle region is more conservative. On the other hand it is likely that sometimes in a fresh specimen the presence of vestigial spots may be ascertained on more segments than in dry specimens or from illustrations.

The type of pattern of figure 1 is met with quite frequently in the genus *Haematopota*, and all the varieties of forms of pattern in Tabanidae can apparently be shown to be only modifications of this *Haematopota*-type. As stated, there are certain species of the genus *Tabanus* in which this pattern occurs in identical form. These are all species of small, at most medium size, among them the American species *T. pumilus*, *sparus*, *vivax*, etc.; it seems that this group comprises the smallest of all known Tabanidae. *T. suffis* (fig. 2), an African species, is of the same very small size and appearance as *H. brunnescens* (smaller than a house-fly!), and shows in its venation a character which is not usually encountered in *Tabanus*, but forms the rule in *Haematopota*. The abdominal pattern likewise recalls *Haematopota*. Here we observe a tendency of the median and subdorsal light spots to become enlarged, the subdorsal ones placed somewhat obliquely, and the median ones assuming a triangular shape with the bases of the triangles resting on the posterior border of the segments, while the lateral spots seem to have shifted to the upper corner of the segments. A series of further modifications frequent in species of *Tabanus* is already indicated here in its initial stages.

T. mordax (fig. 3) affords an example where the lateral spots have wholly disappeared; it is this condition from which the three-banded patterns can be derived, inasmuch as the spots of neighboring segments tend to enter a relation with each other in order to form bands over the whole length of the abdomen. In *Tabanus kingi* (fig. 4) this tendency is already marked; at the same time in segments five to seven a further reduction has taken

place, in so far as here the subdorsal spots have also disappeared and only the median spots remain. In *Tabanus lineola* (fig. 5) we have a type of pattern in which a white dorsal longitudinal band is accompanied by two black bands, and these border again on a white band which in turn is bordered by dark. This pattern may give, as the case may be, the impression of three white bands bordered by black, or of two black stripes on light ground. Frequently, as in *T. costalis*, and in *T. taeniola* (fig. 6) the lateral dark areas are rather light, so that the pattern is further simplified. The dark pigmentation even of the stripes bordering the median light band may be rather pale, so that the whole effect is one of light coloration. From dark gray with three distinct white stripes bordered by black, we have all transitions to a general olivaceous yellow color with a pale yellowish white stripe along the median line, bordered by grayish color hardly darker than the surrounding color.

Another type of modification of the primitive pattern is found when the median light spots have been greatly reduced (*T. lasiophthalmus*, fig. 7), or altogether disappeared (*T. ditaeniatus*, fig. 14). In *T. lasiophthalmus* rudiments of paired black elements are visible on segments three to five and rudiments of white triangular spots on segments three to four. Excepting these spots, the entire median stripe is lacking. On the other hand, the subdorsal spots have been retained on most segments and have been greatly enlarged on segments one and two; here they are placed obliquely, following the same tendency as already indicated in *T. sufis* (fig. 2): their outer contours have become indistinct owing to the diffusion of the lateral spots in their dark background. The disappearance of white spots on a dark background frequently has the effect of lighting up the background in grayish or brownish hues of indistinct boundary, and it is in the nature of the reduction process that these indistinct shades are most often encountered on the sides of the segments, while the middle retains a well-marked pattern.

A third type of modification is that in which the median white spots alone have been preserved, and, subsequently, undergo reduction in number or in size. We have seen in *T. sufis* (fig. 2) how the triangular form of these median spots originates: it is due to the tendency of all dark and light spots (or cross-bands)

to assume an oblique position which leaves a triangular space in the middle of each segment. This alone should indicate that where we have only triangular spots present there must have been originally a whole pattern of the type described. In *T. exul* (fig. 8) we find white triangular spots in the middle of each segment, while the subdorsal and lateral spots are still traceable in the form of ill-defined shades. Probably there are related species which will show them still present. In *Tabanus melanocerus* (fig. 9) the white triangular spots are well marked on all segments while the remainder of each segment has become infuscated. However, dark spots bordering on the white triangles are still plainly visible and even a second row of dark spots is present; between the two a slightly lighter area is included which corresponds to the subdorsal light band of forms like *T. lincola* (fig. 5). In *Tabanus trimaculatus* (fig. 10) no traces of subdorsal or lateral spots are seen, the whole abdomen is uniformly black, but the presence of the typical three white triangular spots on segments three, four, and five requires no further explanation; they are the last remainder of the abdominal pattern of *Hacmatopota* and of *T. suffis*. There are a great many Tabanids in which two or three such white triangles on an otherwise dark abdomen are a conspicuous character (note *T. biguttatus* Wied, a common African cattle-pest). Sometimes the triangles are combined with oblique spots on segments one and two, as already indicated in *T. lasiophthalmus* (fig. 7). From the black abdomen bearing triangles, it is not a long way to a wholly dark abdomen, as in *T. stygius* (fig. 12) a form related to *T. trimaculatus*. Forms like *T. fuscopunctatus* (fig. 11), a Florida species nearly related to *T. exul*, will illustrate the gradual disappearance of the white triangles, leading to uniform black. Needless to say that black as a final result may be reached by different processes of pattern reduction, so that in cases where the abdomen is simply black, we cannot always tell exactly in which way the pattern actually has disappeared. But in forms like *T. stygius* for instance, there is a good deal of likelihood that the black final stage was preceded by a stage marked with the triangles which are still present in the near relatives, and the same thing may be said of *T. giganteus* when compared with its relatives *T. exul* and *T. fuscopunctatus*.

Another series of pattern transformations are the result of a breaking up of the dark background into dark spots. From a glance at fig. 2 (*T. suffis*) it will be evident that the same primitive patterns from which we have started can be taken as the origin of a pattern consisting of dark spots on a light background. Such a pattern, consisting of four rows of black spots, we find on the yellowish-olivaceous abdomen of *T. ditaeniatus* (fig. 13). That this pattern must have had the same origin is all the more evident as the male of *T. ditaeniatus* (fig. 14) has a pattern which represents a modification in the opposite direction, and of a similar type as *T. lasiophthalmus*: suppression of the median row of light spots so that the resulting impression is that of two light subdorsal bands on a dark background. By reduction of dark spots on a light abdomen a uniform light coloration like that of *T. par* (fig. 15) may be derived. There is a considerable variety of indistinctly-shaded abdominal patterns found in species of Tabanidae, of which generally the uniformly light type may be considered an end result.

Turning to the genus *Chrysops*, we find phenomena quite analogous to those described in *Tabanus*. In *Chrysops*, however, generally the initial stage is that of four rows of black spots on a light (yellow or grayish-yellow) background, as exemplified in *C. vittatus* (fig. 16). The same tendency of pattern reduction beginning from both ends of the abdomen, together with fusion of the remaining elements, takes place in *Chrysops*. The pattern variations in *Chrysops* are well known as they serve to distinguish the species. In *C. montanus* (fig. 17) the lateral black spots present in *C. vittatus* have disappeared on segments one and two; on segments three, four, and five they tend to fuse together. In *C. callidus* (fig. 18) the subdorsal black spots on segments one and two separate in *C. vittatus*, and beginning to fuse in *C. montanus*, have fused completely, forming a new characteristic element of pattern. On segments three and four the lateral and subdorsal black spots have fused completely, leaving only narrow light areas open in the median dorsal line. On the following segments black has swallowed everything, and even on segment five, which in *C. vittatus* shows four distinct black spots on light ground, and shows the same spots less distinctly in *C. montanus*, has turned wholly black in *C. callidus*. Finally in *C. sackeni*

(fig. 19) the fused spots on segments one and two have become more rounded and only on segment three a trace of the median light area is left visible. The light borders of all abdominal segments may still preserve a trace of the original light pigmentation.

Another series of changes may be observed in those species of *Chrysops* where the lateral black spots do not fuse with the subdorsal ones but are reduced, and where the subdorsal spots themselves remain apart, leaving a distinct light longitudinal band in the middle of the abdomen. This process begins with *C. obsoletus* (fig. 20) with a pattern easily derived from that of *C. vittatus* (fig. 16), but with the light background somewhat infuscated except in the bright median dorsal area. In *C. univittatus* (fig. 21) frequently the lateral spots have wholly disappeared, while the subdorsal ones have been fused in the longitudinal direction, forming two longitudinal black stripes at both sides of a yellow longitudinal band. Sometimes the whole abdomen with the exception of this light longitudinal band is dark infuscated, or even black. In the sample given of *C. lugens* (fig. 22) a rather variable species, we find the light median band itself in a process of reduction; while, at the same time, on segment two, traces of the light subdorsal spots have been retained.

The African and South American species of *Chrysops* show essentially the same stages of transformation as the North American species. Fig. 23 shows the abdomen of the African *C. fuscipennis* where the fusion of spots in the transverse direction has been carried to an extreme, resulting in an almost wasp-like banded pattern. The South American species *C. omissus* and *C. bulbicornis* (figs. 24 and 25) represent rather primitive types of pattern, not unlike the North American *C. vittatus*. In *C. omissus* a similar tendency to form oblique spots is visible as in *T. suffis*, but the direction of the spots is the opposite in this case.

I have not been able to extend this study to all the exotic forms; however, from the samples I have seen, I find no reason to depart from this argumentation. The South American *Eisenbeckias*, of which so many have been recently described by H. Lutz, show usually a rather simple and therefore derived type of abdominal pattern, not infrequently resulting in transversely banded forms or such with entirely black or brownish abdomen. An interesting case is presented by *Eisenbeckia inframaculata* (figs. 26 and 27) in

which, while the dorsal side is of a clearly derived and much simplified type, the underside shows a spotted pattern which may well be compared with that of a *Chrysops*. However, there are only three rows of spots, the median ones not much larger than the lateral ones. I notice that while in most Tabanids the underside of the abdomen is of a uniform coloration, a number of species, as *T. trimaculatus* and its allies, show a broad, black, median, longitudinal band. If our views are correct, this band represents the last trace of an underside pattern in process of disappearance. The banded, wasp-like patterns are quite frequent among the South American forms, and *Eisenbeckia mattogrossensis* (fig. 28) is only one of the less striking examples. If these views are correct, they have to be considered as derived, not primitive types. The same will hold good for the *Pangonia* group. Here we seldom encounter anything like a primitive pattern. Of the Brazilian forms, *Bombylomyia splendens* (fig. 29) still shows an ill-defined trace of light triangles on a yellowish-brown abdomen, while the abdomen of *Erephopsis nana* (fig. 30) is almost uniformly fuscous, and that of *Erephopsis albitaeniata* (fig. 31) metallic green with whitish borders of the segments. The almost globular form of the abdomen in these bee-like species is itself an indication that we have to deal with derived, not primitive forms of abdominal coloration.

EXPLANATION OF PLATE IX²

² Figs. 1 to 4, fig. 6 and figs. 13 to 15 are drawn after H. H. King, Report on Econ. Ent., Welle. Res. Lab. 111. Report, 1910. Fig. 5, figs. 7 to 12, and figs. 16 to 22 drawn from specimens in my collection. Figs. 23 to 31 from A. Lutz, Notas Dipterológicas, Mem. Instit. Oswaldo Cruz, Rio de Janeiro, 1911.

- Fig. 1.—*Haematopota brunnescens*, ♀.
 Fig. 2.—*Tabanus sufis*, ♂.
 Fig. 3.—*Tabanus mordax*.
 Fig. 4.—*Tabanus kingi*, ♂.
 Fig. 5.—*Tabanus lineola*, ♀.
 Fig. 6.—*Tabanus taeniola*, ♀.
 Fig. 7.—*Tabanus lasiophthalmus*, ♀.
 Fig. 8.—*Tabanus exul*, ♀.
 Fig. 9.—*Tabanus melanocerus*, ♀.
 Fig. 10.—*Tabanus trimaculatus*, ♀.
 Fig. 11.—*Tabanus fuscopunctatus*, ♀.
 Fig. 12.—*Tabanus stygius*, ♀.
 Fig. 13.—*Tabanus ditaeiatus*, ♀.
 Fig. 14.—*Tabanus ditaeiatus*, ♂.
 Fig. 15.—*Tabanus par*, ♀.
 Fig. 16.—*Chrysops vittatus*, ♀.
 Fig. 17.—*Chrysops montanus*, ♀.
 Fig. 18.—*Chrysops callidus*, ♀.
 Fig. 19.—*Chrysops sackeni*, ♂.
 Fig. 20.—*Chrysops obsoletus*, ♀.
 Fig. 21.—*Chrysops univittatus*, ♀.
 Fig. 22.—*Chrysops lugens* var. *morosus*, ♀.
 Fig. 23.—*Chrysops fuscipennis*, ♀.
 Fig. 24.—*Chrysops omissus*, ♀.
 Fig. 25.—*Chrysops bulbicornis*, ♀.
 Fig. 26.—*Eisenbeckia inframaculata*, ♀, ventral side.
 Fig. 27.—*Eisenbeckia inframaculata*, ♀, dorsal side.
 Fig. 28.—*Eisenbeckia matlogrossensis*, ♀.
 Fig. 29.—*Bombylomyia splendens*, ♀.
 Fig. 30.—*Erephopsis nana*, ♀.
 Fig. 31.—*Erephopsis albitaeniata*, ♀.